

LIFE HISTORY OF PEMPHIGUS POPULI-TRANSVERSUS

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INTRODUCTION

The first collection in Louisiana of aphids belonging to the genus *Pemphigus* from the roots of plants of the family Cruciferae seems to have been made on November 19, 1914, by Mr. E. S. Tucker, formerly Associate Entomologist of the Louisiana Experiment Stations. These specimens were taken from cabbage roots (*Brassica oleracea capitata*) at Loranger, in Tangipahoa Parish. Shortly afterwards root aphids of the same genus were noted at Baton Rouge by the writer, and material for identification was submitted to specialists acquainted with the genus. As the stages sent were not recognized as belonging to any described species, and as there were apparently no published records of any species of *Pemphigus* occurring on crucifers in the United States, studies concerning the life history, habits, and economic importance of the species were begun.

After the writer had begun the investigation Maxson (23, p. 501)² published an article on *Pemphigus betae* Doane in which he stated that—

Lice of this genus have been repeatedly taken on turnips in the south.

In a letter to the writer Mr. Maxson has given the additional information that—

the specific instances referred to were brought to my attention by Mr. F. B. Paddock, State Entomologist of Texas, he having sent material to me for identification.

¹ The writer wishes not only to thank Dr. Gillette for his kindness in drawing up the descriptions and supervising the preparation of illustrations, but also for suggestions regarding the biological studies, and especially for the interest which he has taken in the work. Mr. J. J. Davis, of the Bureau of Entomology, and Mr. J. R. Parker, of the Montana Agricultural Experiment Station, also have shown much interest in these studies, and the writer desires to thank them for the aid they have given. Messrs. C. E. Smith and J. L. E. Lauderdale, while members of the Bureau of Entomology, rendered valuable assistance in the studies of the life history and habits of the species.

² Reference is made by number (italic) to "Literature cited," p. 592-593.

Dr. C. P. Gillette also informed the writer that Mr. Paddock sent him material from Texas collected from turnip roots on February 13, 1914, and that the species is the same as that which attacks crucifers in Louisiana. Mr. L. C. Bragg has collected the species from watercress (*Roripa* sp.) near Fort Collins, Colo. Mr. J. J. Davis, of the Bureau of Entomology, has written that several years ago he received a species of *Pemphigus* collected on curly turnip (*Brassica rapa*) at Greenwood, Miss., which seems to agree with the one under discussion.

It is the purpose of this paper to present the results of investigations carried on at Baton Rouge regarding the life history and habits of the species, together with records from other points in Louisiana and from other States. These results indicate that the species of *Pemphigus* that feeds on the roots of crucifers is identical with the well-known *Pemphigus populi-transversus* Riley, which causes galls on the leaf petioles of some of the poplars or cottonwoods (*Populus* spp.). Fortunately, it has been possible to have these notes accompany descriptions of the various stages made by Dr. Gillette.

HISTORICAL REVIEW

While *Pemphigus populi-transversus* has been often referred to by entomological writers since Riley described the species in 1879 (1, p. 15-16; pl. 2, fig. 5, a-c), these references have been brief and for the most part have been limited to records of the occurrence of the species in some State or particular locality and a few words regarding bibliography and the previously recorded hosts and distribution. Such references are mentioned under "Distribution and hosts" on page 580.

In works in which insects are treated especially from an economic standpoint there are several references to the species and its gall. In 1890 Packard (3, p. 434) mentioned it in his work, "Insects injurious to forest and shade trees." Bruner (6, p. 218, fig. 57), included it in an article entitled "Insect enemies of ornamental and shade trees growing in cities and parks," which was published in 1893 in the Annual Report of the Nebraska Horticultural Society, and again mentioned it (11) in an article on aphids which appeared in The Nebraska Farmer in 1901. Lintner (9, p. 361-362) included it in his Thirteenth Report of the State Entomologist of New York, published in 1898, and stated that it had been abundant on *Populus monilifera* in Washington Park, Albany, N. Y., during 1896 and 1897. Felt (14, p. 247, 620, 635-636, pl. 11, fig. 15, 16) in his work, "Insects affecting park and woodland trees," published by the New York State Museum in 1906, also referred to its abundance in the vicinity of Albany and gave colored figures of the gall. Baldwin (21, p. 208) referred to it in the Fifth Annual Report of the State Entomologist of Indiana in 1912 and gave two original illustrations of the gall.

In lists and synopses of North American aphids the species has been mentioned by several authors. It is included in the "Host-plant list of North American Aphididae" by Williams (4, p. 6, 9), published in 1891, and in a bulletin entitled "The Aphididae of North America" by Hunter (10, p. 78), issued in 1901. In a synopsis of the genus *Pemphigus* Jackson (14, p. 182, 183, 206-208) in 1908 referred to the species somewhat in detail and stated that the life history was "very imperfectly known." Further references to its life history have been made by Davidson (16, p. 372) and Gillette and Bragg (22, p. 98). Davidson stated that the stem mothers had been observed "founding their colonies" in the vicinity of Stanford University, California, in March. Gillette and Bragg (22, p. 98) in "Notes on some Colorado aphids having alternate food plants," published in 1916, gave "winter host, *Populus* species; alternate host unknown."

EXPERIMENTS IN TRANSFERRING THE SPECIES FROM CRUCIFERS TO POPLAR AND FROM POPLAR TO CRUCIFERS

Soon after investigational work on this root aphid was begun, winged viviparous females (winged migrants or sexupara), collected from the soil about cruciferous roots, were sent to Dr. Gillette and to Mr. J. R. Parker. Both stated that they did not recognize the individuals as belonging to any described species of the genus *Pemphigus*, but suggested that it was possible that they might be identical with *Pemphigus populi-transversus*. In view of this, experiments were begun in an attempt to ascertain whether there was a migration of the species from crucifers to poplar at one season of the year, and a return migration at another season.

In 1916 cuttings were taken from trees of *Populus deltoides*, before the buds began to swell, and stuck in moist sand in flowerpots, which were kept in a greenhouse. When leaves began to appear on these cuttings, young individuals of the stem mother (fundatrix) were placed on them. These stem mothers had recently issued from eggs obtained in the laboratory from the true sexes, which had in turn been produced by winged females (sexupara) taken from about the roots of crucifers in the field. Swellings soon began to appear on the petioles where the stem mothers had located, and these swellings, increasing in size, gradually took on an appearance typical of the gall of *Pemphigus populi-transversus* (Pl. 82). Unfortunately the stem mothers died after the galls had reached a diameter of about $\frac{3}{8}$ inch. Galls were again formed about stem mothers on leaf petioles of poplar in the greenhouse in the spring of 1917, and these, developing to a greater size, appeared identical to those of *P. populi-transversus*.

During the fall of 1916 winged migrants (fundatrigenia) from the galls of *Pemphigus populi-transversus* were placed under cheesecloth in a cage where turnips were growing. Later, examination of the soil showed the roots of the turnips to be heavily infested with aphids of the genus

Pemphigus, the infestation being similar to that which occurs on cruciferous roots under field conditions. It was evident, when the growth of the plants in this box was compared with that made by plants of the same age in an uninfested box, that they had been affected by the presence of the aphids at their roots (Pl. 84, F). In fact, the turnips died before winged migrants appeared, though probably not altogether because of the insect infestation.

Winged migrants from galls were also placed on turnips growing in pots in the greenhouse. The soil in these pots had been heated previously to a temperature sufficient to kill insect life, and the pots were covered with cloth-covered wire frames. Later, examination showed wingless individuals of *Pemphigus* sp. to be present on the roots, but again the plants died before the winged forms appeared. Before the plants died, however, a number of the wingless aphids were transferred to pots covered with cloth containing cabbage plants, the roots of which had been dipped in a mixture of water and nicotine sulphate before they were planted. On March 2 of the following year winged viviparous females, such as are found in the colonies at the roots of crucifers, were observed. No aphids appeared on the roots of control plants.

These experiments, together with others that have been carried on, indicate that the forms found on poplar and on crucifers belong to the same species. Additional proof is furnished by the fact that from poplar trees in the spring were taken winged viviparous females which agree with winged migrants found at cruciferous roots at that time of the year, and that during late summer and during the fall there were collected from the leaves of crucifers winged viviparous females which are identical with those found in galls of *P. populi-transversus*.

DISTRIBUTION AND HOSTS

The species has been recorded as occurring on poplar in California (16, p. 372; 19, p. 398; 20, p. 699), Texas (1, p. 15-16), Colorado (1; 7, p. 116; 22, p. 98), Kansas (12, p. 22, 23), Nebraska (18, p. 12), Missouri (1, p. 15-16), Iowa (5, p. 130), Minnesota (2, p. 20, 21), Illinois (17, p. 411), Indiana (21, p. 208), New York (9, p. 361-362; 13, p. 247, 620, 635-636; 15, p. 355), and Massachusetts (15, p. 355). Mr. Parker has collected it at Lovell, Wyoming, Dr. Gillette has specimens from Arizona, and Mr. Davis writes that he has records of its occurrence in Wisconsin, Michigan, and Ohio. Mr. H. F. Wilson has taken it in Wisconsin, and the writer has seen galls, apparently made by this species, at Agricultural College, Miss., and Jacksonville, Fla.

Four species of the genus *Populus*, *balsamifera*, *monilifera*, *trichocarpa*, and *fremontii*, have been mentioned as hosts. Britton and Brown (8, p. 491, fig. 1165; p. 493, fig. 1172) give the following distribution for *P. balsamifera*:

Newfoundland to Hudson Bay and Alaska, south to Maine, New York, Michigan, Idaho, and British Columbia.

They give *P. monilifera* as a synonym under *P. deltoides* (the name used in this article), a species which, they state, occurs from Quebec to the Northwest Territory, south to New Jersey, Florida, Colorado, and New Mexico. *P. trichocarpa* and *P. fremontii* apparently occur in the Western States.

FORMATION OF GALLS

In transferring the species from crucifers to sprouting cuttings of *Populus deltoides* it was found that the petioles of young leaves, just out of the bud, are apparently the only ones upon which galls begin to develop. A transverse groove first appears on the petiole where the young stem mother has located, the developing petiole gradually bending at this point. The tissue surrounding the groove, which is on the inside surface of the bent petiole, gradually enlarges until a hollow globular gall, with a transverse slit on the surface opposite the petiole, is formed around the stem mother. Galls found in the field on May 17 were roughly spherical in shape and varied in diameter from $\frac{1}{4}$ to $\frac{1}{2}$ inch. Just before the leaves fall from the trees some of the galls reach a greatest diameter of nearly an inch. The galls vary considerably in shape, length of the transverse slit, and development of the lips (see Pl. 83; 84, A-E). While the general color of the gall is the same as that of the petiole, a portion of the surface often has a reddish tinge.

Practically all of the galls occur somewhere on the leaf petioles, though what seem to be the galls of this species have been found on the new stem growth to which the petioles are attached. The galls usually occur singly, but as many as three have been seen in juxtaposition on one petiole.

In midsummer the gall contains, and indeed is often filled with, the comparatively large stem mother, her progeny in various stages of development, all covered with waxy secretion, together with molted skins and usually with liquid globules.

DATES WHEN GALLS ARE FOUND AT BATON ROUGE

In 1917, at Baton Rouge, winged viviparous females and the true sexes produced by them were taken in a small cavity on the trunk of a poplar tree as early as March 8. These winged females are identical with the winged migrants (sexupara) found about the roots of crucifers. On March 28, young stem mothers were found on leaf petioles where, to judge from the size of the galls, they had apparently been present for a few days only.

During 1916, galls were noted on May 17 which had reached a diameter of $\frac{1}{4}$ to $\frac{1}{2}$ inch. On November 7, when a large percentage of the leaves of the poplar had fallen, few galls remained on the trees.

PERCENTAGE OF LEAF PETIOLES SHOWING GALLS

Leaves were gathered from a tree of *Populus deltoides* on July 26, 1916, to ascertain the percentage of leaf petioles having galls upon them, and to learn whether galls occurred in greatest numbers in any one portion of the tree as regards the height above the ground. Galls are found upon comparatively small trees and upon the largest specimens.¹ The tree selected was about 30 feet in height and the infestation appeared to be an average one for the particular locality. Branches were broken from it at random at various heights. The leaves were then stripped from the branches and counts made of those leaves showing galls and those not infested. It was found that there was a considerable variation in the percentage of leaves showing galls on different branches, but the distance above the ground apparently had no bearing upon the percentage of leaves infested. The results are given in Table I.

TABLE I.—Percentage of leaf petioles of *Populus deltoides* infested with *Pemphigus populi-transversus*, Baton Rouge, La., July 26, 1916

Position of branch on tree.	Number of branches examined.	Number of leaves examined.	Number of leaf petioles showing galls.	Percentage of leaf petioles showing galls.
In approximate lower third	5	222	54	24.3
In approximate middle third	5	441	117	26.5
In approximate upper third	5	512	137	26.7
Total	15	1,175	308	25.2

DATES WHEN WINGED MIGRANTS (FUNDATRIGENIA) ARE FOUND IN GALLS

At Baton Rouge winged females begin to appear in the galls on *Populus deltoides* at a somewhat earlier date than that recorded for other localities. Riley (1, p. 15-16), in connection with his original description of the species, in which he gives Missouri, southern Texas, and Colorado as localities where this species of *Pemphigus* occurs, states that the winged females are "produced in autumn, sometimes not until the leaves have fallen." Williams (18, p. 12) mentions finding winged females, "evidently but lately transformed," in galls at Ashland, Nebr., on September 25. At Baton Rouge, in 1916, winged females were found in the galls as early as June 1, though a very small percentage of the galls contained such individuals on this date. Not until September were they present in more than 10 per cent of rather large collections examined.

¹ Three other species of aphids belonging to the subfamily Pemphiginae have been collected from *Populus deltoides* at Baton Rouge. Of these, *Pemphigus populicaulis* Fitch is the most common, although it is much less abundant than is *P. populi-transversus*. The two other species, found only occasionally in galls which they form on the leaves, have not been identified.

Of 200 galls collected on September 15, 17 per cent contained winged females, while they were present in all of 150 galls taken on September 28.

The number of winged females in a single gall also showed a gradual increase as the year advanced. In June usually only one was found in a gall, while on November 7 as many as 76 were present.

DATES WHEN WINGED MIGRANTS (FUNDATRIGENIA) LEAVE GALLS

Although winged females appeared in the galls at Baton Rouge during 1916 as early as June 1, there is no evidence to show that migration to crucifers took place until late summer. The earliest collection of winged female migrants on crucifer leaves was on August 31, and not until early October were crucifer roots found infested to any considerable extent. On October 2, 1917, during a period of clear, cool, autumn weather, the migrants from the galls were common on turnip leaves at least 500 feet from poplar trees. As many as five were found on the underside of a large leaf. The greatest migration probably occurs during October. While the writer has no definite data regarding the maximum distance they may traverse while in flight, it is probable that they, as well as the sexupara, may be carried long distances by winds.

NUMBER OF WINGLESS VIVIPAROUS FEMALES (VIRGOGENIA) TO WHICH WINGED MIGRANTS (FUNDATRIGENIA) GIVE BIRTH

On October 25, 1916, 25 winged females taken from galls were placed, without food, in vials and kept under observation indoors. All of these began almost immediately to give birth to young, and by October 30 all had died. The average number obtained from each individual was 26, the number ranging from 14 to 37. In one instance a female brought forth 30 young in about 24 hours.

The young viviparous females locate on the roots, feed, and when mature bring forth other wingless viviparous females. In this way the subterranean colonies become established.

INJURY TO AND APPEARANCE OF PLANTS INFESTED WITH SUBTERRANEAN FORMS

While severe *Pemphigus* infestation on the roots of crucifers may be indicated by the wilted condition of the leaves, a slight or moderate infestation does not usually affect, to a noticeable degree, the portions of the plant above the ground. For this reason such infestation usually goes unnoticed. In other words, this insect, while it may cause as much damage as many of those species which feed upon the leaves or other parts of the plant above the surface of the soil, does not attract as much attention as such species because it works out of the sight of the ordinary observer. Inasmuch as these aphids feed upon the roots, it is to be presumed, however, that any infestation is detrimental to the plant.

Upon examination of the soil about plants attacked by the subterranean forms colonies may be found upon any portion of the root system, but the small rootlets appear to be preferred. Where dead leaves, or other trash, occur on the surface of the soil, there is often a growth of rootlets immediately beneath, and colonies are often found in such locations.

Mr. J. L. E. Lauderdale made an interesting observation at Baton Rouge on March 19, 1917, while examining roots of *Coronopus didymus* in a field of stock beets (*Beta vulgaris*). The beets were growing on ridges where the soil was less moist and less compact than that midway between the rows. Of 25 plants of *C. didymus* growing on the ridges, 24 were infested with *Pemphigus populi-transversus*, whereas only 6 of 25 plants growing in the low ground between the rows had aphids present on their roots. This would indicate that either the compactness of the soil between the rows, or its higher moisture content, or both, was disadvantageous to the development of the aphids.

The white, flocculent material which the aphids secrete is of material aid in locating them. This secretion often occurs in considerable abundance about the colonies (Pl. 85). The light-yellow color, characteristic of the bodies of the wingless females, except in their early stages, usually makes it easy to locate them when the soil about the roots on which they are feeding is carefully examined.

INJURY CAUSED BY THE SUBTERRANEAN FORMS

Where the aphids occur in small or moderate numbers at the roots of plants, it is difficult to estimate the amount of damage done by them. The following extracts from correspondence received by the Louisiana Experiment Stations give information as to injury to crucifers by *Pemphigus* spp. in Louisiana. As only wingless forms were forwarded by the correspondents, it can not be stated positively that the root aphid causing the injury was *P. populi-transversus*, although that is probable.

On November 13, 1915, a correspondent living at Rhoda in St. Mary Parish wrote:

I am sending you under separate cover a cabbage plant that is badly infected with a small yellow louse, and would ask if you can recommend anything that can be done. The bug or louse is found at the root of the plant, and seems to suck the sap or eat off the roots, as the plant is badly wilted during the warm part of the day, but revives a little at night, until it finally is killed.

On November 22 of the same year a letter was received from New Iberia, Iberia Parish, in which the writer stated:

Enclosed please find stalk of cabbage with insect at the root that is destroying all my plants.

A report has also been received from Dr. C. E. Mauldin, in charge of the Iberia Live-Stock Experiment Farm of the Bureau of Animal Industry, at Jeanerette, La., that—

It has been necessary for us to abandon the planting of rape and kale at this station on account of the root-louse.

At Baton Rouge the subterranean forms apparently cause more severe injury to turnip than to any other cultivated cruciferous crop that has been under observation. Not only have they been found in greatest numbers on turnips but plants have been frequently noted which, when pulled, came up easily. The roots of these plants were mostly dead, apparently because of the attack of the aphids.

FOOD PLANTS OF THE SUBTERRANEAN FORMS

Wingless specimens of the genus *Pemphigus* have been taken in Louisiana from the roots of the following Cruciferae: Cabbage, turnip, mustard (*Brassica nigra*), cauliflower, and broccoli (*Brassica oleracea botrytis*), Brussels sprouts (*Brassica oleracea gemmifera*), rape (*Brassica napus*), *Coronopus didymus*, *Lepidium virginicum*, and *Roripa* sp. The last three host plants are weeds, the first being common in uncultivated fields at Baton Rouge during the winter months, when the plants are sometimes gathered and used as "greens."

Winged migrants (fundatrigenia) of the species of *Pemphigus* under consideration have been found at the roots of cabbage, turnip, Brussels sprouts, rape, *Coronopus didymus*, and *Roripa* sp. It is quite possible that further observations will disclose the fact that the species occurs also at the roots of plants not belonging to the family Cruciferae. Mr. Lauderdale has found individuals on the roots of stock beet. Adjoining infested roots of *Coronopus didymus* apparently explained their presence on the beet roots, as examination of the roots of many beets, near which no crucifers were growing, failed to disclose additional instances of infestation.

SPREAD OF SUBTERRANEAN FORMS

Observations made in the field and under laboratory conditions indicate that at least the smaller wingless viviparous females (virgogenia) that are present in the soil during the winter months are capable of considerable locomotion, and that when conditions become unsatisfactory, these individuals seek more suitable locations. During December they have been found in great abundance crawling over the surface of the soil and upon the plants in a field of Brussels sprouts. While carrying on some experiments in the greenhouse about a year later, individuals were found to have left flowerpots in which they were feeding on turnip roots, apparently because the turnips had begun to die as the result of being severely infested with the aphid *Myzus persicae* Sulzer. They were

especially numerous on the highest points of the cloth covering these pots, about a foot above the surface of the soil, and could be easily dislodged by slight puffs of air. Some were found under conditions which indicated that they were about 3 feet away from the nearest point where they could have originated.

As the season advances, the wingless viviparous females give birth to individuals which develop into winged viviparous females (sexupara), which later leave the soil and fly away.

DATES WHEN WINGED MIGRANTS (SEXUPARA) ARE FOUND IN THE SOIL

A few winged females have been found in the soil as early as December 12, and, as is the case with the winged females occurring in the galls, their number gradually increases as the season advances. During 1917, roots of *Coronopus didymus* were examined in the field from time to time with the idea of ascertaining how late in the spring the species occurs in the soil. The last winged individuals were taken on April 9. On April 16 no subterranean forms could be found, though winged migrants were alive on poplar as late as April 30.

From the field observations it appears that these winged migrants fly from the crucifers to the poplar trees during the spring, where, usually in some suitable crevice, they give birth to the true sexes. Winged females, agreeing with the winged females found about cruciferous roots, were found in such locations on poplar trees during March and April, 1917. Some observed on March 20 were dead, with true sexes and eggs located near by.

NUMBER OF YOUNG TO WHICH WINGED MIGRANTS (SEXUPARA) FROM CRUCIFERS GIVE BIRTH

In the laboratory, under conditions quite different from those under which the winged migrants would live in the field, the greatest number of sexed individuals to which a single aphid was observed to give birth was six. Usually this winged form brings forth all of her offspring within a short time and then dies. Those kept in the laboratory were examined daily, all of the young usually being produced from the time of one examination to the next. Individuals of both sexes have come from one winged migrant.

Examination of the abdomens of several winged migrants, collected from soil about the roots of crucifers, showed them to contain from four to seven sexed specimens, seven being the predominating number.

DEVELOPMENT OF THE TRUE SEXES (SEXUALES)

Eggs have been obtained in the laboratory from true sexes kept without food. The number of molts which the males and females undergo has not been ascertained, nor has it been learned when copulation takes

place. The female is larger than the male and deposits only a single egg. In a well-ventilated insectary at Baton Rouge, during 1916, eggs were first noted on March 6 in vials in which the true sexes had first appeared 12 days before.

OVIPOSITION

The egg is often found resting in a small amount of white, cottony material secreted by the female. The true sexes apparently do not, as a rule, move far from their places of birth, eggs being found in the field in crevices on the trunks and limbs of poplar trees where living winged migrants (sexupara) and the dead bodies of others were present. In the insectary at Baton Rouge stem mothers were first seen on March 22, 1916, in vials where eggs had first been noted on March 6, giving a period of 16 days for the incubation of the egg.

FORMATION OF GALL

Of necessity the young, active stem mother (fundatrix), after issuing from the egg, must make its way to the developing leaves, where it settles down on the petiole and becomes responsible for the formation of a gall. While there is no absolute proof that such is the case, it is believed from field observations that one stem mother is responsible for one gall only and that a gall is only formed when a young stem mother locates on a leaf petiole.

SEASONAL HISTORY OF PEMPHIGUS POPULI-TRANSVERSUS IN BRIEF

The following summary has been prepared from observations made in the field and laboratory at Baton Rouge (fig. 1). The dates when the various stages appear and migration takes place probably depend to some extent upon the weather. It would be interesting to know the seasonal history of the species in the northern portion of its range where climatic conditions, especially as regards temperature, are so different from those existing in Louisiana.

The galls begin to develop on the petioles of the young leaves of *Populus deltoides* in the spring. They increase in size during the summer and by the time the leaves fall in the autumn some have reached a diameter of nearly an inch.

Of 1,175 leaves gathered from a poplar tree on July 26, 1916, 26.2 per cent had galls on their petioles. They occur on both small and large trees.

Winged migrants (fundatrigenia) have been found in the galls as early as June 1. The percentage of galls containing winged migrants, as well as the number found in any one gall, increases as the season advances.

Winged migrants from the galls fly to various cruciferous plants. They have been found on the leaves of such plants as early as August 30 and as late as October 31.

The winged migrants give birth to viviparous females (virgogenia) which start colonies on the roots of crucifers, upon which they feed.

The infestation at the roots of crucifers, which is usually made apparent by the white, cottony material which the aphids excrete, gradually becomes more severe, owing to the increase in the number of the subterranean forms. It appears that, under certain conditions, the smaller, wingless viviparous females occurring in the soil are able to migrate to a considerable distance from their place of birth and there begin new colonies.

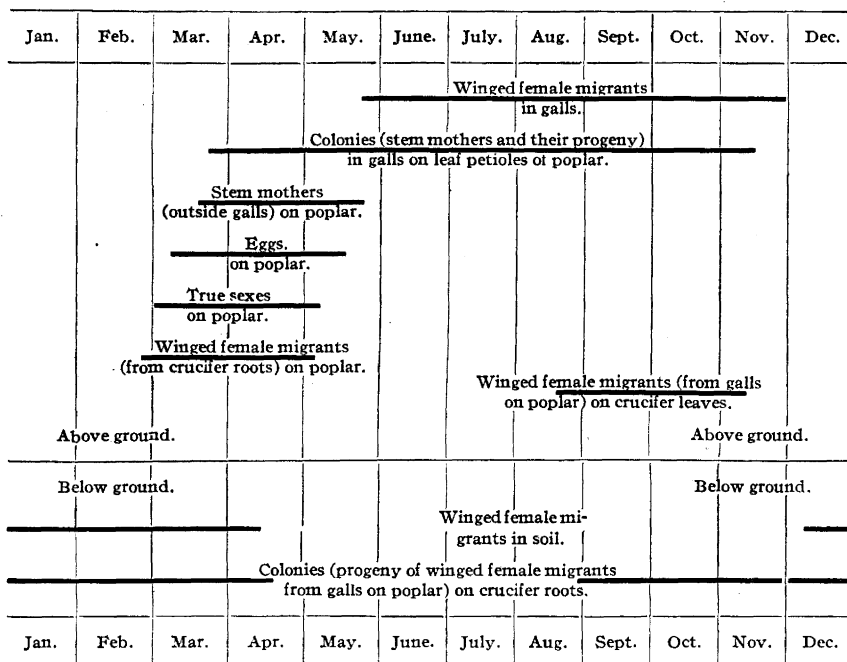


FIG. 1.—Diagram illustrating the seasonal history of *Pemphigus populi-transversus* at Baton Rouge, La.

Winged migrants (sexupara) appear in the subterranean colonies during the winter. They have been found at the roots of cabbage, turnip, Brussels sprouts, rape, *Coronopus didymus*, and *Roripa* sp. Colonies of a species of *Pemphigus* have also been found at the roots of mustard, cauliflower, broccoli, and *Lepidium virginicum*. No winged migrants were present in these colonies, but it appears probable that the aphids were of the same species.

In the spring the winged migrants fly from the crucifers to poplar trees where they give birth to the true sexes (sexuales), usually in crevices on the trunks and branches.

The sexed individuals take no food and, after pairing, the female deposits a single egg.

The stem mother (fundatrix), after issuing from the egg, makes its way to the young leaves of the poplar, where it settles down on a petiole. Here a gall begins to form about it.

DESCRIPTIONS OF STAGES OF PEMPHIGUS POPULI-TRANSVERSUS AND ITS GALL

By C. P. GILLETTE

Examples of this species in the collection of the Colorado Experiment Station, which were collected by Mr. J. T. Monell at St. Louis, Mo., on October 2, 1907, agree in every particular with Riley's description of the winged form, except that the fifth joint of the antenna is not quite as cylindrical as the description would indicate. Specimens sent by Mr. T. H. Jones, of the Bureau of Entomology, which were collected from similar galls at Baton Rouge, agree perfectly with the Missouri specimens, and with specimens taken at many different times in Colorado. Winged and wingless "lice" taken by Mr. E. S. Tucker, then of the Bureau of Entomology, from the roots of turnips at Baton Rouge, on March 6, 1915; by Mr. F. B. Paddock, State Entomologist, on turnips, at College Station, Tex., on February 13, 1914; and by Mr. T. H. Jones on Brussels sprouts at Baton Rouge, on March 4, 1916, agree well in structural details.

The galls are widely distributed over Colorado upon the broad-leaved cottonwoods; but they are not abundant, except upon an occasional tree. It should be stated here that the sexupara of this species is separated with some difficulty from the same form of *Pemphigus betae*. In the latter species, however, the permanent sensorium of joint 5 is of the normal form and never broad and irregular, inclosing chitinous islands, as in *populi-transversus*, and the spur is distinctly longer.

FUNDATRIX, FIRST INSTAR.—Described from specimens reared by Mr. T. H. Jones at Baton Rouge, La., and taken from the galls on March 3, 1916.

Ground color pale yellow tinged with green; head black; wax plates dusky; length, 0.60 mm.; width, 0.23 mm.; antenna, 0.45 mm., 4-jointed, joints 1, 2, and 3 subequal in length, joint 4 with spur, almost as long as 2 and 3 combined and very stout, and with several transverse rows of small chitinous points; all femora stout, the greatest width of the hind femur nearly equalling one-half its length; six longitudinal rows of wax plates upon the dorsum of segments 1 to 6 of the abdomen, and four rows of larger plates upon the dorsum of the thorax, each plate bearing at least one short, stout hair; legs and antennæ deep shining black with a few short stout gray hairs (Pl. 81, A).

ADULT FUNDATRIX.—Described from living specimens taken at Fort Collins, Colo., by Mr. L. C. Bragg, Assistant Entomologist of the Colorado Experiment Station, on September 22, 1916, from galls on leaves of *Populus deltoides*. The opening of the gall was a straight, transverse, or somewhat diagonal slit, passing from one-half to two-thirds of the way across the gall, but not a narrow and protruded mouthlike or liplike

opening. The galls at this date appeared to be fully grown. Besides the stem mother, there were, in each gall, a few winged "lice" quite dark in color, a good number of pupæ of varying sizes, the small ones being quite pale in color, and numerous small larvæ which were very light colored and heavily tufted with white waxy threads. The old gall mother seemed to be the sole parent of the gall colony, all of which normally acquire wings.

The stem mothers were a yellowish sordid green in color, very plump, covered with a fine white powder; head, the entire legs, including coxæ, and tips of the antennæ dusky to blackish; antenna 4-jointed and very short, not as long as hind tibia, in length approximately 0.40 mm.; length of body 2.50 to 3 mm.; joint 3 distinctly longer than joint 4 with spur, the proportion being about as 3 to 2; length of hind tibia 0.50 mm.; eyes very small. There are upon the dorsum six longitudinal rows of rather large wax plates beginning upon the mesothorax and extending to the seventh abdominal segment. Upon the prothorax and the eighth abdominal segment the number of plates is reduced to four (Pl. 81, C, H).

The writer also examined, in connection with this description, numerous specimens taken in Louisiana by Mr. T. H. Jones, in California by Messrs. E. Bethel and George P. Weldon, in Arizona by Mr. Bethel, and on the eastern and western slopes of the mountains in Colorado by Messrs. L. C. Bragg and C. P. Gillette.

It seems certain that the wingless stem mother that starts the gall of this species early in the season normally continues to feed and reproduce until the leaves mature in the fall, all of her young acquiring wings and going in search of the alternate food plants of the family Cruciferae.

FUNDATRIGENIA MIGRANT FROM THE GALLS.—In color and general appearance like the winged sexupara from turnips and Brussels sprouts. The specimens examined average about 0.25 mm. shorter in body length. The differences in the antennal segments are quite marked. Joint 3 has from two to six transverse sensoria, the usual number being three or four. Joint 4 is the shortest and weakest and rarely has a small sensorium. Joint 4 being somewhat smaller, and joint 5 slightly larger than in the sexupara, the contrast in size of these segments is very noticeable. The permanent sensoria on joints 5 and 6 are very large and irregular, and even may be cut into two by projecting chitinous margins. They always have upon their surfaces small chitinous pieces, one or two on joint 5 and two to four on joint 6, each bearing one or more short hairs. Upon joint 6 this large irregular sensorium may extend from the base of the spur to the middle of the segment and is nearly always very irregular in outline. The proportions of the segments are about as follows: 1, 21; 2, 30; 3, 66; 4, 31; 5, 39; 6 with spur, 68. There are many irregularities in the antennæ of this species, one of which is the frequent union of segments 3 and 4 into one (Pl. 81, J).

WINGLESS VIVIPAROUS FEMALE.—Described from specimens taken by Mr. T. H. Jones at Baton Rouge, La., from the roots of Brussels sprouts, on April 2, 1917.

General color sordid pale yellow, with head, antennæ, and legs dusky brown to blackish; tarsi and eyes black; length 2.50 mm.; width 1.60 mm.; antenna 0.45 mm., joints 3, and 5 plus spur, subequal; joint 4 much the shortest, being less than one-half as long as joint 3; beak barely attaining second coxæ; hind femora and tibiae

each 0.55 mm.; body and legs very free from hairs; apparently no wax glands on the body (Pl. 81, E, I).

PUPA.—Almost uniform pale lemon yellow with slight greenish tinge on abdomen and a shade of flesh color upon the thorax; wing pads very slightly dusky along the outer margins; head, antennæ, and all the legs dusky; eyes black.

WINGED SEXUPARA.—Described from living specimens taken by Mr. T. H. Jones, Baton Rouge, La., on March 21, 1917, bred from Brussels sprouts, and from preserved specimens from Mr. F. B. Paddock, College Station, Tex., which were taken on February 2, 1913; from Mr. E. S. Tucker, Baton Rouge, La., taken on March 5, 1915, on turnips; and from one specimen taken by Mr. L. C. Bragg, near Fort Collins, Colo., on watercress (*Roripa* sp.) on August 31, 1917.

Head, antenna, entire thorax above, mesothorax below, and entire legs black; wings slightly smoky, with subcostal vein black or blackish and heavy along the inner or lower margin of the stigma; abdomen sordid light greenish yellow without markings; body everywhere with a slight covering of gray powder; dorsum of abdomen covered more or less with a cottony secretion; length of body 2 mm.; wing 2.70 mm.; antenna 0.60 mm.; hind tibia 0.75 mm.; joints of antenna in following proportions: 1, 22; 2, 30; 3, 65; 4, 32; 5, 32; 6 with spur, 56; sensoria transverse, joint 3 with four to eight, usually five or six; 4 with two or three; 5 and 6, normally, with permanent sensoria only; spur near base of joint 3 distinct. Permanent sensorium on joint 5 usually very large, often inclosing one or two chitinous pieces as in fundatrigenæ. Nervures of wing dusky, the costal and subcostal being heavy and black; stigma blackish, nearly parallel sided, and about three times as long as broad (Pl. 81, D, K).

OVIPAROUS FEMALE.—Described from a number of specimens deposited in a cage in the laboratory by specimens sent by Mr. T. H. Jones, from Baton Rouge, La.

General color buttercup yellow, with head, antennæ, and legs whitish and very transparent; a little dusky on the vertex; eyes black; antennæ short, 0.15 mm. long, 4-jointed, joints subequal, the first, and last including the spur, longest; length of body 0.70 to 0.90 mm. (Pl. 81, G).

EGG.—Oblong oval, glistening, varying in color from dull white to yellow. Ten eggs, deposited in the laboratory, averaged 0.54 mm. in length, ranging from 0.48 to 0.57 mm., and 0.21 mm. in width, ranging from 0.19 to 0.24 mm.

MALE.—Described from specimens born along with the oviparous females.

The males differ from the females by being pale yellowish green in color, more slender in form, and a little shorter, 0.60 to 0.65 mm. long, the legs very stout (Pl. 81, F).

GALLS.—Riley described the gall of this species as follows:

Formed upon the petiole near the base of the leaf of *Populus monilifera* and *P. balsamifera*. An elongate-oval swelling, causing the curving and broadening of the petiole, and opening on the opposite side by a transverse slit, with a whitish, slightly thickened, and elevated margin, recalling human lips.

The writer has studied large numbers of galls of this species from Colorado and Louisiana, the latter collected by Mr. T. H. Jones. When fully grown, they vary normally from about 12 to 18 mm., extra sizes attaining 20 or even 25 mm. in their greatest diameter, which is usually

in the direction of the petiole of the leaf. The fundatrix, or stem mother, soon after hatching from the egg, locates upon the petiole of a very young opening leaf, causing it to curve and thicken, and form a transverse groove (Pl. 81, B, a, b, c) at the point of attack. The petiole continues to thicken, and the groove to deepen, forming a pit or groove which carries the "louse" with it, and the two margins or lips gradually meet, inclosing the "louse" in a spacious cavity. The mouth or slit is usually transverse, but may be turned more or less in a vertical position, and the margins may, or may not, be thickened or protruded. By the time the inmates become mature and ready to fly, the lips separate enough to allow the "lice" to pass out in search of the alternate food plants. The expanded petiole of the leaf can be easily seen extending along the convex surface of the gall opposite the mouthlike opening. (For typical forms of this gall, see Pl. 82; 84, A-E.)

The gall of this species is readily separated from the galls of *Pemphigus populicaulis*, which have a long curved opening formed by the twisting of the petiole upon itself, or from the galls of *P. populi-ramulorum*, which develop upon the side of tender growing twigs (Pl. 84, A-E).

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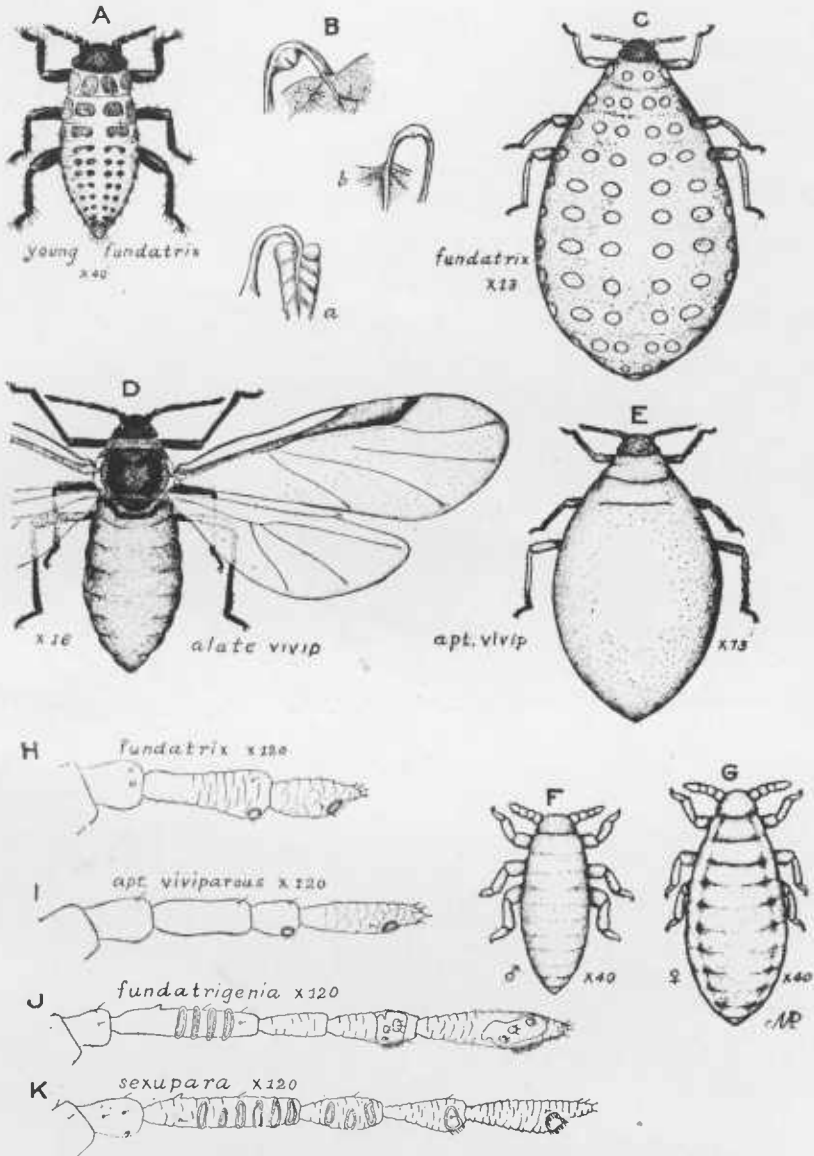
¹ More recently the writer has learned that as early as 1902 Dr. F. H. Chittenden recorded the receipt of specimens of an unknown species of *Pemphigus* from Texas. These were sent by Mr. S. A. McHenry, of the Beeville Substation of the Texas Experiment Stations, on February 14, 1901, with the information that the species was doing injury to the roots of cabbage in the vicinity of Beeville, some of the fields being reported as totally destroyed. (CHITTENDEN, F. H. SOME INSECTS INJURIOUS TO VEGETABLE CROPS. U. S. Dept. Agr., Div. Ent., Bul. 33, n. 3, p. 79. 1902.)

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PLATE 81

Pemphigus populi-transversus:

- A.—Young fundatrix, first instar. $\times 40$.
 - B, a, b, c.—Beginning of galls on cottonwood leaves.
 - C.—Adult fundatrix with cottony secretion removed. $\times 13$.
 - D.—Winged sexupara from roots of Brussels sprouts. $\times 16$.
 - E.—Wingless virgogene from roots of Brussels sprouts. $\times 13$.
 - F.—Male. $\times 40$.
 - G.—Oviparous female. $\times 40$.
 - H.—Antenna of fundatrix. $\times 120$.
 - I.—Antenna of wingless viviparous female from Brussels sprouts. $\times 120$.
 - J.—Antenna of winged fundatrigenia from gall. $\times 120$.
 - K.—Antenna of winged sexupara from Brussels sprouts. $\times 120$.
- Drawn by Miss Miriam A. Palmer.



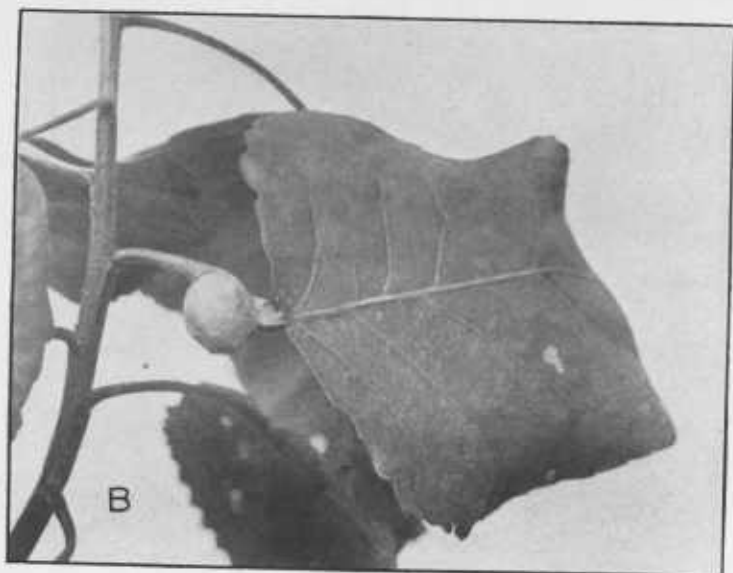
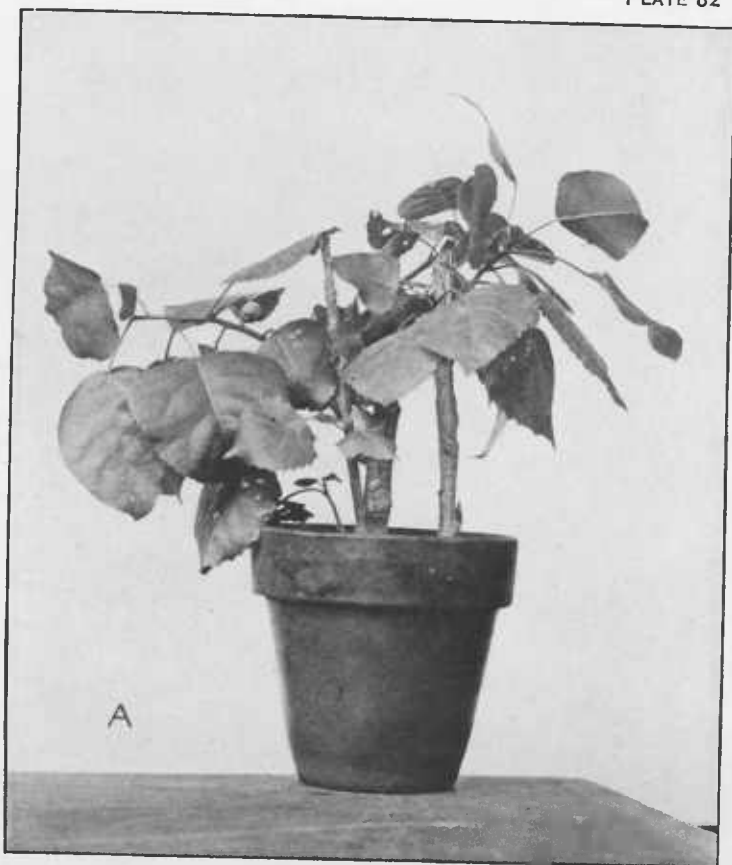


PLATE 82

Pemphigus populi-transversus:

A.—Gall on poplar cutting. Cuttings were collected before the buds began to swell and were planted in sand in flowerpots kept in a greenhouse at Baton Rouge, La. Young stem mothers of *Pemphigus populi-transversus*, obtained indirectly from winged female migrants from roots of crucifers, were placed on growing cuttings on March 23, 1916. The photograph, taken on May 27, shows pot containing cuttings. One developing gall can be seen on twig at upper left.

B.—Gall shown in A, enlarged to nearly natural size. Beside it can be seen the slit of a small gall which has failed to develop to any considerable extent.

PLATE 83

Pemphigus populi-transversus:

Variation in size of galls and location on leaf petioles of *Populus deltoides*, Baton Rouge, La., September 15, 1916. About natural size. Shows lips of galls all protruding, and in some cases thickened.

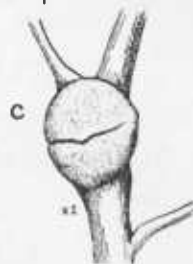


Pemphigus populi-transversus

Pem. p-transversus



PLATE 84
Pem. p-ramulorum



Pem. p-caulis

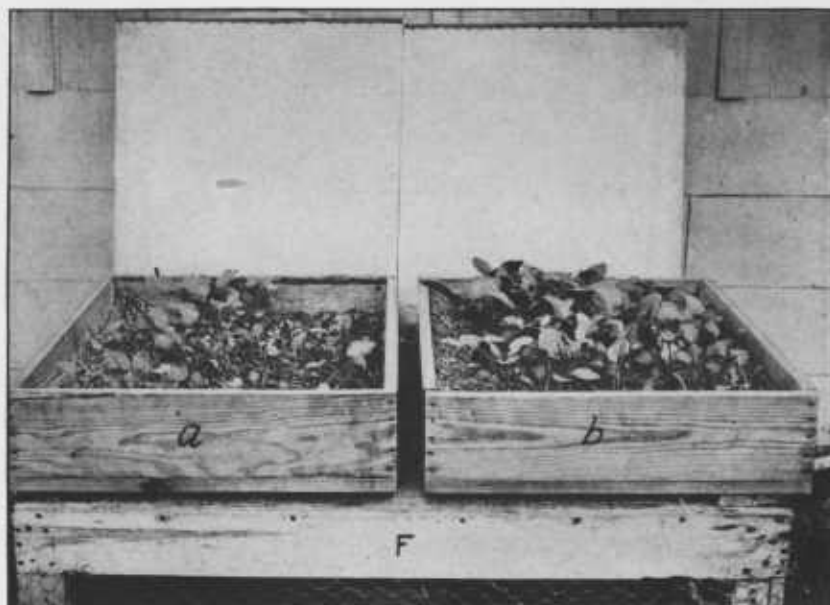
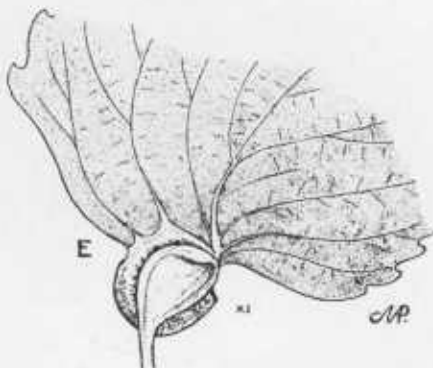
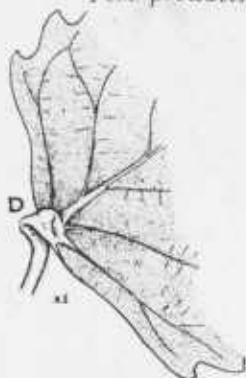


PLATE 84

A.—Gall of *Pemphigus populi-transversus*, lips not protruding.

B.—Gall of *Pemphigus populi-transversus*, lips protruding.

C.—Gall of *Pemphigus populi-ramulorum*.

D.—Beginning of gall of *Pemphigus populicaulis*.

E.—Full-grown gall of *Pemphigus populicaulis*.

All natural size. Drawn by Miriam A. Palmer.

F.—Turnip seedlings, showing injury by *Pemphigus populi-transversus*: a, infested; b, control. Turnips were planted at Baton Rouge, La., on September 16, 1916, in boxes having cloth-covered tops. Galls of *P. populi-transversus* were placed in box a on September 28. Photographed on October 13, at which time the wingless form of the aphid was abundant on roots of plants in box a. No root aphids found in box b. Note difference in growth of plants in the two boxes.

PLATE 85

Pemphigus populi-transversus:

F.—White cottony secretion at roots of Brussels sprouts due to presence of *Pemphigus populi-transversus*. Photographed at Baton Rouge, La., on February 10, 1916.

